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Abstract

Species and cultivars of the genus *Rhamnus* and related genera in the Rhamnaceae were tested for their suitability as overwintering hosts of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae). The tests were carried out in outdoor cages during the fall through spring of 2002–2003 and 2003–2004. Response of the aphid to the hosts varied from successful overwintering on three *Rhamnus* hosts to complete rejection of all species in other genera. Fall migrants (gynoparae), egg layers (oviparae), males and eggs were found on the exotic *Rhamnus cathartica* (L.), and native *Rhamnus alnifolia* L'Héritier and *Rhamnus lanceolata* Pursh. In the spring eggs hatched, colonies developed and spring migrants were produced on these hosts. Other *Rhamnus* spp. were accepted by fall migrants and some level of colony development occurred, but no overwintering eggs were deposited on them. The phenology of the production of the various morphs, egg deposition, and egg hatch are documented on the suitable hosts. The implications of our findings on soybean aphid ecology and management are discussed.

Keywords

Aphis glycines, *Rhamnus*, buckthorn, soybean aphid winter host

Disciplines

Agricultural Science | Agriculture | Entomology | Horticulture

Comments

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Potential Winter Hosts of Soybean Aphid

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ABSTRACT Species and cultivars of the genus *Rhamnus* and related genera in the Rhamnaceae were tested for their suitability as overwintering hosts of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae). The tests were carried out in outdoor cages during the fall through spring of 2002–2003 and 2003–2004. Response of the aphid to the hosts varied from successful overwintering on three *Rhamnus* hosts to complete rejection of all species in other genera. Fall migrants (gynoparae), egg layers (oviparae), males and eggs were found on the exotic *Rhamnus cathartica* (L.), and native *Rhamnus alnifolia* L'Héritier and *Rhamnus lanceolata* Pursh. In the spring eggs hatched, colonies developed and spring migrants were produced on these hosts. Other *Rhamnus* spp. were accepted by fall migrants and some level of colony development occurred, but no overwintering eggs were deposited on them. The phenology of the production of the various morphs, egg deposition, and egg hatch are documented on the suitable hosts. The implications of our findings on soybean aphid ecology and management are discussed.

KEY WORDS *Aphis glycines*, soybean aphid winter host, *Rhamnus*, buckthorn

THE SOYBEAN APHID, *Aphis glycines* Matsumura (Hemiptera: Aphididae), a pest of soybean, *Glycine max* (L.) Merrill, was first recorded in North America during summer 2000. The soybean aphid has a heteroecious holocyclic life cycle, alternating sexual reproduction on its “primary hosts,” which include several species in the genus *Rhamnus*. Parthenogenic reproduction occurs on its “secondary hosts,” including soybean, other *Glycine* species, *Pueraria phaseoloides* (Roxb.) Benth (tropical kudzu), and *Desmodium intortum* (Miller) Urban (Wang et al. 1962, Takahashi et al. 1993, Voegtlin et al. 2004). The soybean aphid feeds and reproduces viviparously on secondary hosts during the summer and then develops winged morphs called gynoparae that migrate to primary hosts in the fall. Gynoparae produce wingless morphs called oviparae, which are subsequently mated by winged males migrating from secondary hosts. Eggs are laid adjacent to twig buds or on bark crevices, where they overwinter. Wingless fundatrices hatch from eggs in the spring and begin colonies that produce winged morphs that migrate to secondary hosts, completing the life cycle.

The relative distribution of primary and secondary hosts influences aphid dynamics and pest status in soybean (Wang et al. 1962, Takahashi et al. 1993, Raggsdale et al. 2004). Aphid infestations in soybean in areas

with concentrations of a primary host tend to begin earlier in the season and at higher densities than fields located some distance from overwintering sites. The timing of infestation in soybean is of particular relevance, because earlier infestations more often lead to higher aphid densities (Raggsdale et al. 2004), yield loss (Wang et al. 1996, van den Berg et al. 1997, R.J.O., unpublished data), and insecticide use (Wang et al. 1994a, b). The lack of data on soybean–primary host relationships, particularly the identity of primary hosts and the relative distribution of primary hosts and soybean fields, significantly limits predictive capabilities for pest management purposes.

The genus *Rhamnus* is placed within the Rhamnaceae, which contains >50 other genera (Smith 1977). Other than *Rhamnus* species, no other members of the Rhamnaceae have been evaluated for their ability to support overwintering by the soybean aphid. There are >100 species of *Rhamnus*, most of which are native in temperate regions of the Northern hemisphere (Rehder 1940, Smith 1977). Several species are common in the United States, and often the most prevalent species have become naturalized here after being introduced from Europe or Asia. For example, *Rhamnus cathartica* (L.), a Eurasian species known to be a primary host of the aphid in both Asia (Wang et al. 1962, Takahashi et al. 1993) and the United States (Raggsdale et al. 2004), is present in large populations in midwestern soybean-producing areas. *Rhamnus* spp. are important components of the native flora of the United States, but other than *Rhamnus alnifolia* L'Héritier (see Voegtlin et al. 2004) none has been evaluated for its suitability as a primary host of the soybean aphid.

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In this article, we report the result of a field-cage study on the overwintering host plants of the soybean aphid. Putative host plants were selected based on their taxonomic affinity, their current or future potential prevalence in major soybean-producing U.S. states and growth forms. We also compare information on soybean aphid overwintering success in field collections to our cage results.

Materials and Methods

We studied 11 taxa of the Rhamnaceae family: seven *Rhamnus*—*Rhamnus cathartica*, *Rhamnus frangula* (L.), *Rhamnus caroliniana* Walter, *Rhamnus alnifolia*, *Rhamnus lanceolata* Pursh, *R. frangula* 'Asplenifolia', and *R. frangula* 'Columnaris'—and four species in different genera—*Ceanothus americanus* L., *Berchemia scandens* (J. Hill) K. Koch, *Hovenia dulcis* Thunberg, and *Rhamnella franguloides* (Maximowicz) Weberbauer. Nine species and two cultivars of *R. frangula* were tested in the first year. In the second year *R. cathartica* from Illinois and *R. caroliniana* from Ohio, Oklahoma, and Missouri were included. The origins of each species are as follows: *R. cathartica*, Eurasia; *R. frangula*, Eurasia and Africa; *R. caroliniana*, southeastern United States; *R. alnifolia*, northern United States; *R. lanceolata*, east central United States; *Rhamnella franguloides* and *H. dulcis*, Asia; *C. americanus*, eastern United States; and *B. scandens*, southeastern United States. (Rehder 1940, Smith 1977). All plants were grown by W.R.G. in Iowa and carried to the Illinois Natural History Survey in Champaign, IL, where the tests were conducted.

Eight 2 by 2 by 2-m walk-in cages were set up on recently tilled ground and the edges buried. In mid-September, one of each test plant was randomly placed around the inside perimeter of the cage. Plants in the cages were of different sizes reflecting their growth forms and cultivation. For example, *R. cathartica*, *R. frangula*, *R. frangula* Asplenifolia and Columnaris, and *R. caroliniana* were in large (25–28-cm-diameter) pots. *B. scandens*, *H. dulcis*, *C. americanus*, and *Rh. franguloides* were in 18-cm pots, and *R. lanceolata* and *R. alnifolia* were in 10-cm pots. Some of the larger plants with hundreds of leaves reached the top of the cage, whereas others like *R. lanceolata* and *R. alnifolia* were <10 cm in height, some specimens with only a few leaves. No attempt was made to standardize the size of plants within or between cages.

Four soybean plants infested with hundreds of soybean aphids were placed in the center of each cage in mid-September. No attempt was made to be certain that all cages had an equal number of aphids. All test hosts were examined twice each week and the number of gynoparae, oviparae, males, and eggs were counted. Plants were examined until all aphids died and plants became dormant. Once dormant, plants indigenous to areas with relatively mild winters (*Rh. franguloides*, *B. scandens*, and *H. dulcis*) were moved into a cold chamber for the winter and were returned to the cages in late March. The remaining test plants, with greater

resistance to low temperatures, were kept outdoors and buried to the level of the soil in the pots.

Spring observations were begun at the end of March and continued semiweekly through mid-May. Fundatrices, second-generation apterae and winged migrants were recorded. In April 2003, soybean was placed in a few cages to document colonization by migrants. To determine the number of eggs that survived the 2003–2004 winter, we removed twigs on 1 April 2004 from each of the three host species on which eggs were deposited in the cages. Eggs were counted and categorized as hatched, unhatched, and collapsed. We calculated the percent egg hatch and used contingency table χ^2 analysis to compare the percentage of egg hatch across host plant species. We assumed all collapsed and unhatched eggs were dead and would fail to hatch. We used the method of Arnold (1960) to compute the day-degrees development of eggs in the month eggs hatched (March of both years). Temperature data were obtained from the Illinois State Water Survey (Water and Atmospheric Resources Monitoring, <http://www.sws.uiuc.edu/warm/>) for Champaign, IL, and we used bases of 5 and 10°C in day-degree calculations. Finally, in early May 2004, 30 newly matured alatae were collected and released in a small cage in which a soybean plant and small plants of *R. lanceolata* and *R. alnifolia* had been placed. Observations were made on host plant selection and colony development by these spring migrants.

Results

No aphids were observed on *B. scandens*, *H. dulcis*, *C. americanus*, or *Rh. franguloides*. Gynoparae settled on all the species and varieties in the genus *Rhamnus* and produced oviparous nymphs on *R. cathartica*, *R. caroliniana*, *R. frangula*, *R. alnifolia*, and *R. lanceolata*. The nymphs matured to oviparae and eggs were deposited only on *R. cathartica*, *R. alnifolia*, and *R. lanceolata* (Table 1). We noted no eggs or colonies on *R. lanceolata* in the first year of study.

Egg survival ranged between 83 and 87% (Table 2). We found no significant difference in percentage of egg hatch among the three host species ($\chi^2 = 4.69$, $df = 2$, $P = 0.10$). First instar fundatrices were observed on opening buds on 26 March 2003 and on 27 March 2004. The buds on *R. lanceolata* and *R. alnifolia* opened a few days earlier than those on *R. cathartica*, and nymphs were first observed on these two native hosts. Assuming nymphs had hatched no earlier than 25 March, the day-degree totals up to this date with 5°C as base were 76.2 in 2003 and 55.3 in 2004. Using a base of 10°C, the day-degree totals for the same time period were 26.1 in 2003 and 11.1 in 2004.

Fundatrices were observed reproducing in the second week of April. Fourth instar alataid nymphs were first observed in colonies during the third week of April in both 2003 and 2004, 3 and 4 wk after egg hatch, respectively. Spring migrants were present in both years from the third week of April until the colonies were gone in late May. Alates were observed feeding and reproducing on *R. cathartica* in most cages and on *R. caroliniana* in one of the cages. In addition, spring

Table 1. Morphs of *A. glycines* observed on putative host plants during the fall and spring

Plant host	Aphid morphs observed	
	Autumn	Spring
<i>R. cathartica</i>	Gynoparae (8, 8), males (8, 5), oviparae (8, 4), eggs (8, 4)	Fundatrices (8, 4), apterae (8, 4), alatae (8, 4)
<i>R. frangula</i>	Gynoparae (8, 1), males (2, 0), oviparae (2, 0) ^a	
Asplenifolia	Gynoparae (1, 0)	
Columnaris	Gynoparae (7, 3), males (4, 0)	
<i>R. caroliniana</i> – Oklahoma	Gynoparae (8, 3), males (6, 0), oviparae (2, 0) ^a	
<i>R. alnifolia</i>	Gynoparae (8, 7), males (7, 7), oviparae (7, 7), eggs (5, 7)	Fundatrices (5, 7), apterae (5, 7), alatae (5, 7)
<i>R. lanceolata</i>	Gynoparae (7, 8), males (3, 8), oviparae (2, 8), eggs (0, 7)	Fundatrices (0, 7), apterae (0, 7), alatae (0, 7)
<i>Rh. franguloides</i>		
<i>H. dulcis</i>		
<i>C. americanus</i>		
<i>B. scandens</i>		
Additional host plants added in second year		
<i>R. cathartica</i> –Illinois	Gynoparae (8), males (6), oviparae (8), eggs (6)	Fundatrices (6), apterae (6), alatae (6)
<i>R. caroliniana</i> –Ohio	Gynoparae (2) ^b	
<i>R. caroliniana</i> –Oklahoma	Gynoparae (2) ^b	
<i>R. caroliniana</i> –Missouri	Gynoparae (2), oviparae (1) ^b	

The number in parentheses indicates the number of plants (out of eight) upon which the morph was observed in 2002 and 2003, respectively, for autumn morphs, and 2003 and 2004, respectively, for spring morphs. A blank indicates no morph(s) were observed.

^a Only oviparous nymphs observed.

^b Only four plants were available from each of these locations.

migrants released into a cage that contained *R. lanceolata*, *R. alnifolia* and soybean settled and produced colonies on *R. lanceolata* and soybean.

Discussion

A. glycines shows a clear preference among potential primary host plants. Gynoparae settled only on species and cultivars in the genus *Rhamnus*, and no aphids were observed on non-*Rhamnus* species. The lack of colony development and egg deposition on *R. lanceolata* in the first year may have been due to the

condition of test plants that year: plants had dropped their leaves early in the fall that year, before oviparae or eggs were produced. On *R. frangula* and *R. caroliniana*, nymphs are produced by the gynoparae, but they do not reach maturity (Table 1). The cultivars of *R. frangula* (Asplenifolia and Columnaris) seem to be of different quality, because gynoparae were found only once on Asplenifolia (a single gynoparae on one plant), whereas Columnaris plants were more commonly infested (Table 1). In our collections of aphids in the field, we have found gynoparae and nymphal oviparae on *R. frangula*, suggesting possible evolution toward

Table 2. Counts of eggs observed on twigs removed from *Rhamnus* spp. on 1 April 2004

Egg condition ^a		No. eggs per twig					
		<i>R. lanceolata</i>					
Hatched	99	164	102	127	75		147
Unhatched	7	5	12	34	10		15
Collapsed	8	3	7	13	13		21
% hatched ^b	87	95	84	73	77		80
Avg % hatch		87.3					
		<i>R. alnifolia</i>					
Hatched	90			103		198	
Unhatched	5			19		15	
Collapsed	9			2		7	
% hatched ^b	87			83		90	
Avg % hatch		85.1					
		<i>R. cathartica</i>					
Hatched	70	65	82	91	107	65	115
Unhatched	3	23	7	6	6	8	6
Collapsed	12	11	0	8	3	4	7
% hatched ^b	82	66	92	87	92	84	90
Avg % hatch		82.8					

^a Eggs were classified as hatched, unhatched, or collapsed.

^b Percentage of hatch was calculated by dividing the number of eggs hatched by the total eggs and assumes none of the unhatched eggs would have subsequently hatched.

use as a winter host (D.J.V. and R.J.O., unpublished data). Continued exposure and attempts at fall survival on this species may eventually lead to its acceptance as a viable primary host of the soybean aphid.

Eggs showed high survival over the 2003–2004 winter (Table 2). The lack of consistency of day-degree calculations between years may reflect differential development of eggs before the month they eclose or evidence of possible diapause. Egg hatch, however, was simultaneous to bud break in all three suitable *Rhamnus* spp. Because eggs are difficult to find in situ, whereas bud break is easy to observe in *Rhamnus*, the correspondence of bud break and egg hatch may provide soybean aphid managers a means to estimate when aphids are emerging from their overwintering egg state. Further research on egg developmental rates and survival over additional winter conditions is suggested.

The production of spring migrants occurs during the time soybean is being planted in Illinois. The success of migrants in finding soybean will depend on when they are produced and the percentage of soybean acreage planted at the time of migration. For example, by 2 May, <10% of fields in 2003 and 2004 were planted with soybean (Illinois Agricultural Statistics 2004), and migrants at this time may have difficulty finding soybean to infest. Alternatively, although the 5-yr average of planting dates for Illinois shows that ≈50% of fields are planted by 20 May (Illinois Agricultural Statistics 2004), many of the colonies of migrants in our cages were gone. Although some “early” spring migrants would find newly emerged soybean, other aphids may continue to reproduce on their buckthorn hosts, as we observed for both *R. cathartica*, *R. lanceolata*, and in one cage on *R. caroliniana*. The observation of spring migrants initiating colonies on *R. caroliniana* is surprising as successful development of oviparae did not occur on this host in the fall. Those settling back on buckthorn and reproducing will extend the time colonies exist on the winter host and subsequently produce additional winged aphids that can migrate in search of soybean. In addition, other host species such as red clover, *Trifolium pratense* L. (Hill et al. 2004), which is widely available in the landscape in early spring, may serve as a “bridge” between aphid production on primary hosts and the widespread availability of soybean in the spring. However, we have been unable to document the use of *T. pratense* by the soybean aphid in the field (D.J.V., unpublished data). The impact of the temporal overlap of primary and secondary hosts on soybean aphid survival and colonization of soybean awaits further study.

The two native primary host plant species, *R. lanceolata* and *R. alnifolia*, are of limited numbers and distribution and as such they unlikely play a significant role in the dynamics and pest status of the soybean aphid. In contrast, *R. cathartica* is widely distributed and often exists in very large numbers in certain parts of the soy-

bean-growing region of the United States and Canada. As such, it is most likely the principal overwintering host of the aphid in North America, and the primary host species of most importance to the aphid's pest status in soybean.

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